

ON *Ankyrodrilus*, A NEW GENUS OF BRANCHIOBDELLID
WORMS (Annelida)

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In the course of my studies of the branchiobdellids of North America, it has become evident that certain materials previously considered as representative of species of *Xironodrilus* Ellis, 1919, (Holt, 1951) cannot be assigned to this genus. It seems fitting, therefore, since the new species involved will be mentioned in a forthcoming paper on the crayfishes and their commensals of the Mountain Lake region of Virginia, to erect a new genus for these species and present diagnoses of them.

In order to prepare the way for the treatment which follows of the proposed new genus, brief references to the genera *Xironodrilus* and *Xironogiton* Ellis, 1919, are necessary.

The distinguishing characteristics of the genus *Xironodrilus*, as diagnosed by Ellis (1919), are the depressed body form, the straight gut with enlargements in segments III and IV, nine segments visible in dorsal view, glandular disks on the lateroventral margins of segments VIII and IX, and the opening of the anterior nephridia by separate pores on the dorsum of segment III. Other features mentioned by Ellis are either common to several genera of the branchiobdellids or of doubtful taxonomic utility. The other, mostly brief, published references to *Xironodrilus* add nothing pertinent to the present discussion. My unpublished dissertation (Holt, 1951), however, treated the type species, *X. formosus* Ellis, 1919, and the other species at that time assigned to the genus, in some detail. In particular, the reproductive systems were described at length and the position adopted in this paper is based upon inter-species variation in these systems.

The genus *Xironogiton* was established by Ellis (1919) on the basis of, among other characters: the presence of an "accessory sperm tube", the reduction of segment IX so that in dorsal view the body appears to be composed of eight or fewer segments, a "loop", or "loops", of the gut in segment VII with its maximum enlargement in segment V, and a depressed and laterally expanded condition of segments V through VIII which confers a "tennis racket" shape upon the body. The nephridial openings are as in *Xironodrilus*. I studied the reproductive systems of

Xironogiton instabilis (Moore, 1894) and pointed out that this species does not have an accessory sperm tube (Holt, 1949). It does, however, show certain affinities with the species included in the new genus proposed here.

The materials were handled by methods that have been previously described (Holt, 1960a), except that most of the animals were collected in 70% alcohol instead of alcohol-formalin. My catalog numbers for collections are indicated by the initials PCH.

Acknowledgements. — Part of the material included herein is taken from a thesis submitted to the Graduate Faculty of the University of Virginia in partial fulfillment of the requirements for the degree of Doctor of Philosophy. Later studies have been supported by grants from the National Science Foundation (NSF G-4439, G-9828, and GB-372). I am indebted to Dr. Horton H. Hobbs, Jr., not only for guidance in the early stages of my studies of the branchiobdellids, but for continuing encouragement and the identification of all host cryfish.

Genus *Ankyrodrilus*¹, n. gen.

Type-species — *Ankyrodrilus koronaeus*, n. sp., here designated.

Diagnosis — Branchiobdellid worms with two pairs of testes; paired nephridiopores on the dorsum of segment III; at least nine distinct segments visible in dorsal view; gut straight, with sacculations in segments II, III, IV, those of segments III and IV the larger; aggregations of gland cells present in lateral portions of segments VIII and IX; caudal sucker ventral; body depressed and tapering gradually from anterior end to its greatest width in segment VI, VII, or VIII; spermiducal gland large, with blindly ending bifurcated proximal portion, vasa deferentia entering the median portion of the organ; bursa constricted between atrial and penial sheath portions, giving to organ as a whole a reduplicated aspect; ejaculatory duct absent; spermatheca composed of ectal duct, bulb, and ental process.

Distribution and affinities. — The distribution of the genus *Ankyrodrilus* is presented below for the included species. Available information indicates that this genus is composed of disjunct populations found in the southern portions of the Interior Plateau and Valley and Ridge physiographic regions of the Southeastern United States.

As is apparent from the discussion above of *Xironodrillus* and *Xironogiton*, these two genera include the closest known relatives of *Ankyrodrilus*.

¹ From *ankyra*, Gr., anchor, and *drilos*, Gr., penis, by extension, worm; *anchorworm* from the anchor-shaped ental end of the spermiducal gland; of masculine gender.

The only really diagnostic characters mentioned by Ellis (1919) which separate the former two genera are the greater number of segments incorporated into the ventral sucker and the "looped" gut of *Xironogiton* as opposed to the greater number of apparent body segments and the straight gut with anterior sacculations in *Xironodrilus*. (In these respects, *Ankyrodrilus* cannot be separated from *Xironodrilus*). My unpublished data, however, clearly separate these genera on the basis of differences in the reproductive systems and I have previously described, — a description which I now know is applicable to all members of this genus, — the reproductive system of *Xironogiton instabilis* (Holt, 1949). *Ankyrodrilus* differs from *Xironogiton*: (1) in the greatly elongated and expanded penial sheath of *Ankyrodrilus* as opposed to the shorter, thicker walled, and asymmetrical bursa of *Xironogiton* (Holt, 1949); (2) in the proximal bifurcation of the spermiducal gland of *Ankyrodrilus*; from *Xironodrilus* (1) in the position of the points of entry of the vasa deferentia into the spermiducal gland, ental in *Xironodrilus* (Holt, 1951), and along the midlength of the gland in *Ankyrodrilus*; and (2) in the greatly developed bursa of the latter as opposed to a small, spherical one in *Xironodrilus*.

***Ankyrodrilus koronaeus*², n. sp.**

(Figs. 1, 4-14)

Diagnosis. — Upper jaw with three large teeth, subequal in length; lower jaw convex, rounded at tooth-bearing border, carrying four small, subequal teeth.

Description. — *Ankyrodrilus koronaeus* differs from the new species described below in the form and dentition of the jaws. There is little variation in the shape of the jaws and the arrangement of the teeth; occasionally the upper jaw has a smaller extra tooth to the side, but this never obscures the very characteristic shape of this jaw. The same remark applies to the lower jaw. A detailed description of the anatomy of *A. koronaeus* is given below as representative of the genus as presently known.

Type-locality. — Roanoke River, 4.5 miles east of Blacksburg, Montgomery County, Virginia. July 4, 1949. H. H. Hobbs, Jr. (PCH 240d).
Hosts: *Cambarus bartoni bartoni*, *Cambarus montanus acuminatus*.

Disposition of types. — The holotype, U. S. National Museum No. 30874 and six paratypes, U. S. National Museum No. 36875 are deposited in the United States National Museum. Two paratypes are retained in my collection (PCH 240d).

Distribution. — In addition to the type locality, *A. koronaeus* is known

² *koronaeus*, a latinized anagram of Roanoke; named for the Roanoke River.

from thirty-two other collections from streams of the Roanoke, James and New River drainage systems in the counties of Montgomery, Giles, Craig and Botetourt, Virginia. Hundreds of specimens are included in these collections and a detailed report on them will be included in the forthcoming paper mentioned above (Hobbs, Walton and Holt).

Ankyrodrilus legaeus³, n. sp.
(Figs. 2-3)

Diagnosis. — Upper jaw with five teeth; lower jaw with four-five teeth; teeth of upper jaw of unequal length, lateral teeth and median teeth shorter than others; lateral teeth of lower jaw longer than median teeth.

Description. — There appears to be little variation in the structure of the jaws and the dentition of this species; features that readily distinguish it from *A. koronaeus*. In other respects *A. legaeus* is very similar to its congener.

Type-locality. — Four miles east of Ewing, Lee County, Virginia. August 18, 1948. J. T. Wheeler. Host: *Cambarus* sp. (PCH 139).

Disposition of types. — The holotype, U. S. Nat. Mus. No. 30872 and four paratypes, U. S. Nat. Mus. No. 30873 are deposited in the United States National Museum. Three paratypes (PCH 139) are retained in my collection.

Distribution. — In addition to the type locality, *A. legaeus* is known from the following localities: TENNESSEE: *Overton County*. Holt Spring Branch, tributary to Eagle Creek, approximately four miles northeast of Livingston. November 8, 1946, and subsequent dates. P. C. Holt. Host: *Cambarus tenebrosus*. (PCH 13, 29, 59, 60, 61, 264, 680). VIRGINIA: *Giles County*. Wolf Creek on Route 61 at city limits of Narrows. June 18, 1961. H. H. Hobbs, Jr. Host: *Cambarus bartonii bartonii*. (PCH 1442). *Lee County*. Tributary of Powell River, four miles west of Ewing. August 24, 1948. J. T. Wheeler. Hosts: *Cambarus* sp., *Cambarus parvovulus*. (PCH 140). Eleven miles west of Jonesville on State Route 58. June 16, 1950. H. H. Hobbs, Jr. and C. W. Hart. Hosts: *Cambarus* sp., *C. parvovulus*, *C. longulus longirostris*, *C. carolinus*. (PCH 371 and 372). Straight Creek at Pennington Gap on State Route 70. June 17, 1950. Hobbs and Hart. *Cambarus* sp., *Orconectes rusticus forceps*. (PCH 373). Three miles north of Pennington Gap on State Route 70. June 17, 1950. Hobbs and Hart. Host: *Cambarus* sp. (PCH 374). One mile north of Gaylor on Dry Run. September 3, 1951. Hobbs. Hosts: *Cambarus bartoni* subsp., *C. parvovulus*. (PCH 530). *Pulaski County*. Intersection of Routes 738 and

³ *legaeus*, a latinized anagram of eagle, for Eagle Creek, Overton County, Tennessee.

640 at confluence of Track Fork and Big Shuffle Branch to form Peak Creek. July 6, 1962. J. E. Carico and E. P. McConnell. Host: *Cambarus bartonii bartonii*. (PCH 1557)

Remarks on the anatomy of *Ankyrodrilus*

The description of *A. koronaeus* which follows is taken with only minor revisions from my unpublished dissertation (Holt, 1951) and, since it is based on a good series of serially sectioned animals, the opportunity is taken here to describe in some detail features of general anatomical and histological interest in the study of the branchiobdellids. As determined by a study of whole mounts, these data apply also to *A. legaeus*.

Both transverse and longitudinal sections, prepared by the usual paraffin embedding method and stained with Delafield's hematoxylin, counter stained with eosin, as well as a large series of whole mounts, were used in this study.

The body form of the members of the genus *Ankyrodrilus* is similar to that of species of *Xironodrilus*. The head is very slightly less in diameter than segment I; the sucker is somewhat greater in diameter than either the head or segment I. The peristomium in both species is set off from the remainder of the head by a sulcus and is distinctly less in diameter. It is divided into upper and lower lips without lobes or tentacles, although occasionally the lower lip of *A. legaeus* may have a median emargination. The maximum body width is usually in segment VII. As an indication of size, the following measurements of four mature individuals of *A. koronaeus* mounted entire is presented: *total length*, 1.99-2.72 mm. (average 2.49 mm); *maximum width*, 0.59-0.80 mm. (average 0.69 mm); *head width*, 0.27-0.36 mm. (average 0.32 mm.); *segment I, diameter*, 0.28-0.35 mm. (average, 0.33 mm.); *sucker diameter*, 0.25-0.43 mm (average, 0.35 mm.). Specimens of *A. legaeus* are of comparable size.

The segments are clearly distinct and the major annulations of the segments are of greater diameter than the minor ones (fig. 6); but supernumerary muscles of the major annulations which account for the raised condition of these annulations in *Ellisodrilus durbini* (Ellis) (Holt, 1960b) are absent. The differences in diameter of the major and minor annulations in *A. koronaeus* are produced by minute attachments of the strongly developed longitudinal muscles to the inner edge of the sulci delimiting the annulations of a segment.

Franzén (1962) has recently pointed out that the muscle cells of *Xironogiton instabilis* are "hirudinean" in character rather than like those of the oligochaetes as Schmidt (1903) thought. Franzén's remarks apply in general, to all the branchiobdellids, so far as I know, and certainly to the North American members of the group, including *Ankyrodrilus koronaeus* and *A. legaeus*.

The anterior nephridiopores can be recognized in serial sections as very minute paired openings in the body wall located dorsolaterally on segment III. The outlet ducts of the nephridia can be traced in whole mounts to this location, but the actual openings cannot be seen.

An opportunity to study in sections the so-called lateral disks or cups of segments VIII and IX which apparently are identical to those described for *Xironodrilus formosus* (Ellis, 1919) confirm the opinion already formed from the study of whole mounts of specimens of species of *Xironodrilus* that these structures are not depressions as Ellis thought, but ovate aggregations of gland cells that open on the lateral margins of the segments mentioned. These gland cells are distinct from the gland cells of the epidermis of the body wall and the clitellar region and the multicellular glands that open in the anal and sucker region. They are very narrow cells with a minute amount of protoplasm, and a nucleus at the inner proximal end and elongated distal ductules. The ductules are filled with granules of secreted material and open in a group onto the lateral margins of the laterally expanded segments VIII and IX. The lateral location of these glands reminds one of the lateral glands of *Bdellodrilus illuminatus* (Moore, 1895), but there is little in their finer structures to indicate a relationship with these glands of the later species.

The jaws of the species of *Ankyrodrilus* show little or no intra-species variation. In *A. koronaeus*, the median tooth of the three teeth of the upper jaw (fig. 5) is shorter than the lateral ones, but the convexity of the jaw is such that the points of the teeth form an essentially straight line. The lower jaw (fig. 4) has teeth that are subequal in length, though the convexity of the jaw causes the middle ones to project beyond the two lateral teeth. In *A. legaeus*, the upper jaw has five teeth that are of unequal length: the lateralmost and the median teeth are shorter than the other two. The lower jaw of this species bears normally four teeth, exceptionally five, of which the lateralmost are the longer. These differences are constant and readily apparent. The individual variations I have seen, quite a few in many specimens, never obscure the basic differences in jaw shape and dentition between these species.

The segmental location of the anus in the branchiobdellids has been in dispute (Moore, 1895; Ellis, 1919). An effort to determine the location of the anus in *A. koronaeus* was made. Externally it appears to open on the posterior surface of segment IX. Internally, the septum separating segments VII and VIII is well developed and a less definitely defined septum, consisting mainly of two layers of peritoneum, separates segments VIII and IX. There is no intersegmental septum 9/10; instead, the longitudinal muscles that go into the formation of the sucker here become evident as strands that cross the coelom and more posteriorly fill,

along with the acetabular glands, the body cavity. The thin septum 8/9 meets the rectum dorsally only a very short distance anterior to the anus. The anus of *A. koronaeus* opens, then, on the dorsum of segment IX, as does that of *Xironodrillus pulcherrimus* (Moore, 1894) and *X. formosus* (Holt, 1951) in spite of Ellis' (1919) belief that the anus of the latter species opens at the intersegmental furrow between segments IX and X. There are no loops of the rectum in *A. koronaeus* and the rectal portion of the gut lies anterior to the anus, contrary to the condition that Ellis (1919) described in *X. formosus*.

Male reproductive system. — The testicular segments are tightly packed with spermatocytes and spermatozoa and there is nothing of unusual interest in reference to the testes.

Located in the usual position, postero-laterally in segments V and VI, the male funnels (figs. 1 and 8) are prominent, elongate, funnel shaped structures with the open ends only slightly flared. They range in the specimens measured from 61.1 to 73.4 microns in length (average 66.0 microns). A funnel (fig. 8) is composed of a single layer of epithelial cells with indistinct cell boundaries and at its fundus where the peritoneal covering of the efferent duct ends there is a widening of the lumen. Except for the slightly larger average size of the funnels of this species, they closely resemble those of *Xironogiton instabilis* (Holt, 1949). They differ from those of the latter species mainly in shape, not being so distinctly campanulate.

The efferent ducts (figs. 1 and 13) are ensheathed by the peritoneum, as is true of other branchiobdellids (Holt, 1949), but this covering is more easily detected in *A. koronaeus* than is usual. The course of the efferent ducts are indicated in figure 1 and it is only necessary to call attention to the fact that there is no connection of the posterior pair with septum 6/7 and that they pierce the peritoneum of the ventral body wall and unite under the nerve cord close to the bursa to form the posterior vas deferens. The anterior pair of efferent ducts pierce the peritoneum at the point where they pass through septum 5/6 at the ventro-lateral margin of the coelom in segment V. In size the ducts of this species are rather large, ranging from 14.7-21.2 microns (average 18.3 microns) in diameter.

The vasa deferentia are remarkable for their shortness and the fact that they hardly equal in diameter that of the parts of the efferent ducts that are free in the coelom, ranging from 14.7-19.6 microns (average 17.3 microns) in diameter. They do not appear to differ histologically from the efferent ducts. They enter the spermiducal gland near its mid-length, just posterior to the bursa. The anterior one enters laterad and farther from the ectal end of the spermiducal gland than does the posterior one.

The spermiducal gland of the genus *Ankyrodrilus* is a conspicuously large organ of a most unusual shape (fig. 1). It is approximately equal to the width of the segment in length and either lies transversely in segment VI or, if disposed longitudinally, is bent upon itself. The ental end is peculiar in being roughly T-shaped, with the cross of the "T" composed of the same glandular epithelium as the rest of the organ and differing only in that the extreme ends of the organ are capped by flattened cells resembling somewhat the bulbular ental end of the prostate gland in some species of the genus *Cambarincola* (Holt, 1949; Hoffman, 1963) and other branchiobdellids (Holt, 1960a, 1960b). There are no apparent differences in the staining reactions of the different regions of the spermiducal gland as there are in *Xironogiton instabilis* (Holt, 1949), but the spermiducal gland of *A. koronaeus* differs from that of *X. instabilis* in the apparent absence of a covering layer of muscle: no muscle elements were found in the peritoneal covering of the gland (fig. 10). An idea of the size of the spermiducal gland is given by measurements of the greatest diameter which ranges from 47 to 82 microns in seven specimens (average 69 microns).

An ejaculatory duct, as I have defined this structure elsewhere (Holt, 1949, 1960a), is absent in *A. koronaeus* and its congener.

The bursa and penis of the species of *Ankyrodrilus* are most unusual, perhaps even more distinctive of the genus than the specializations of the spermiducal gland. The branchiobdellid bursa consists of an ectal atrium and an ental penial sheath enclosing the penis, which is a protrusible cone in some genera, an eversible tube in others (Holt, 1960a). In the absence of observations of the everted bursa and its actual functioning, the interpretation of the bursal complex of *Ankyrodrilus* is difficult. Ectally there is an approximately spherical region (figs. 1 and 9) which appears to be homologous with the atrial region of other genera. In genera with an eversible bursa there is an inwardly projecting fold of the atrial region which forms the rim of the everted cup-like bursa. In the species of *Ankyrodrilus*, this atrial fold has the appearance of a protrusible penis (fig. 9) and may actually function as such. Entad to this portion the bursa is an elongated and often expanded muscular sac carrying at its junction with the spermiducal gland another penis-like projection. This projection appears to be homologous with the penis of other branchiobdellids. But, it is far from clear that it functions as such. A study of the complex outer longitudinal (in reference to the organ) and inner circular muscles of the inner part of the bursa suggests that the atrial region is non-eversible and that the penial sheath region is eversible. In this case, the innermost projection (the true penis) would be carried to the outside as a protrusible penis. But, on the other hand, the inner portion (penial sheath) of the bursa may serve as a "pumping" organ with the outer projection (the atrial fold) carried to

the outside as a functional penis by the eversion of the atrial region. The arrangement of the musculature of the bursa (fig. 7 and 9) is perhaps consonant with either interpretation. In any case, the specializations of the male efferent apparatus of these species are distinctive and in themselves justify the erection of a separate genus to include the species possessing them.

Female reproductive system. — The ovaries form paired masses located dorsoanteriorly in segment VII and are attached to the posterior face of septum 6/7 at each dorsolateral margin by a muscular pedicel resembling those of *Xironogiton instabilis* (Holt, 1949). The oögonia radiate from this point of attachment. A large maturing egg is usually present, filling most of the coelomic space of segment VII. The vascular loops described by Moore (1895) are present, passing around the posterior part of each ovary. In all these respects, then, the ovaries are similar to those of other branchiobdellids.

The ovipores (fig. 12) resemble in all respects those described by Moore (1895) for *Bdellodrilus illuminatus* and *B. philadelphicus* (= *Cambaricola philadelphica*), but lack the cilia reported for *Xironogiton instabilis* (Holt, 1949).

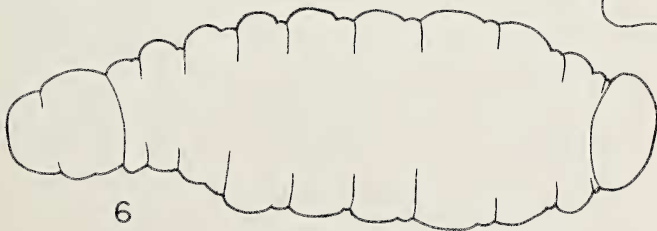
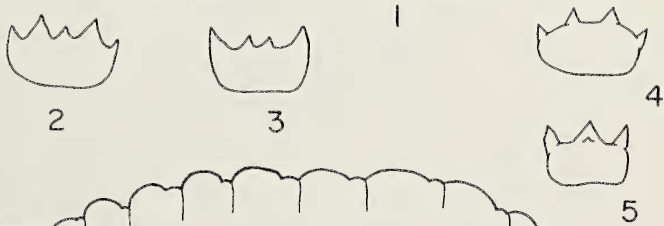
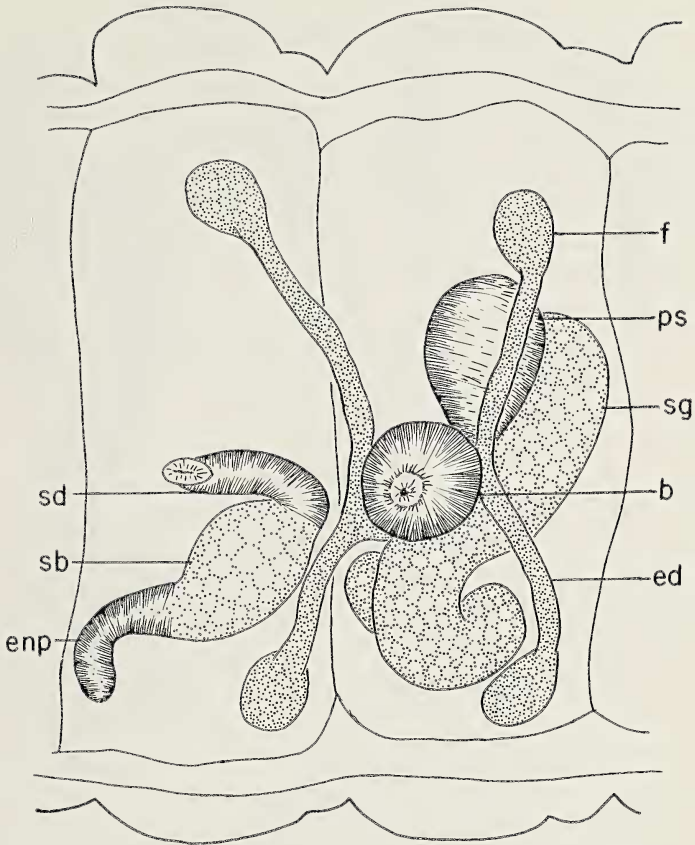
The spermatheca (figs. 1, 11, and 14) of *Ankyrodrilus koronaeus* and *A. legaeus* is divided into three sections. The ectal spermathecal duct (figs. 1 and 11) is subdivided into an ectal region (fig. 11) and a more ental portion. The first of these regions corresponds to the spermathecal bursa known for some species (Holt, 1960a and unpublished data). The ental region of the spermathecal duct is the duct proper. It is lined with a glandular epithelium composed of long cells tapering towards the lumen of the organ (fig. 11). Spermatozoa are not found in this region. The spermathecal bulb, in which spermatzoa are stored, is in its histology much like that of other branchiobdellids (fig. 14). There is a narrowed ental process of the spermatheca, in which spermatozoa are not found, but differing little in histology from the bulb. The entire organ is invested by a peritoneal covering and a thin layer of muscles.

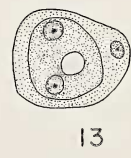
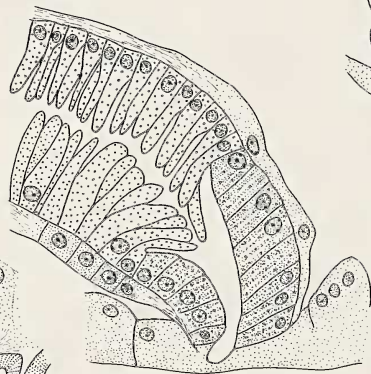
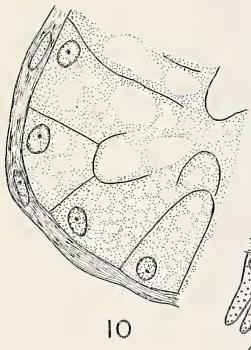
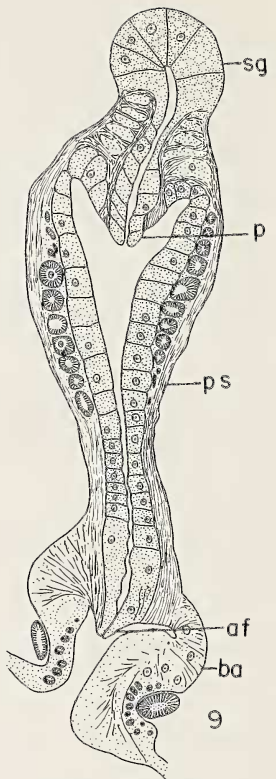
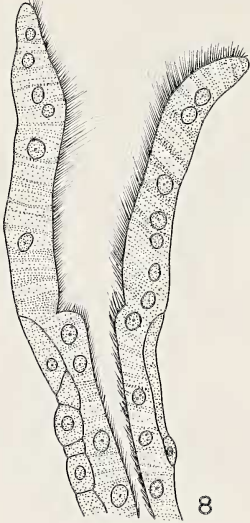
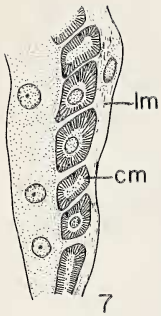
Summary

The new species, *Ankyrodrilus koronaeus* and *A. legaeus*, of branchiobdellid worms from Virginia and Tennessee are described and the new genus *Ankyrodrilus* erected to receive them. *Ankyrodrilus* differs from *Xironogiton* in the bifurcated spermiducal gland and elongated bursa of *Ankyrodrilus* as opposed to the tubular spermiducal gland and flattened, short bursa of *Xironogiton*; from *Xironodrilus* in the medial points of entry of the deferent ducts into the spermiducal gland and the spherical bursa of *Xironodrilus*. A brief description of the anatomy of *Ankyrodrilus koronaeus* is presented.

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EXPLANATION OF FIGURES

All figures were drawn with the aid of a camera lucida.

Legend. *af*, atrial fold of bursa; *ba*, atrium of bursa; *cm*, circular muscles of bursa; *f*, male funnel; *ed*, efferent duct; *enp*, ental process of spermatheca; *lm*, longitudinal muscles of bursa; *p*, penis; *ps*, penial sheath of bursa; *sb*, spermathecal bulb; *sd*, ectal duct of spermatheca; *sg*, spermiducal gland.

Fig. 1. *Ankyrodrilus koronaeus*, ventral view of reproductive organs of segments V and VI.

Figs. 2 & 3. *Ankyrodrilus legaeus*, upper and lower jaws, respectively.

Figs. 4 & 5. *A. koronaeus*, lower and upper jaws, respectively.

Fig. 6. *A. koronaeus*, ventral view of animal.

Figs. 7-14. *Ankyrodrilus koronaeus*, histological details of reproductive systems: 7, detail of bursal wall in longitudinal section showing arrangement of muscles; 8, male funnel in longitudinal section; 9, longitudinal section of bursa; 10, detail of histology of spermiducal gland; 11, detail of ectal duct of spermatheca in longitudinal section; 12, section through ovipore; 13, cross section of efferent duct; 14, detail of wall of spermathecal bulb in section.